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Perceptual learning of apparent motion mediated through ON- and OFF-pathways in human vision

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Abstract

We document the performance of 26 human observers practicing a motion discrimination task in foveal vision. Two blocks of 1960 apparent motion stimuli each were presented in succession. Stimuli in the two blocks were tailored to activate either the ON-pathway (ON-stimulus) or the OFF-pathway (OFF-stimulus). Initial performance of about half of the subjects was rather weak but improved with practice. Initial performance of the other subjects remained unaffected for the first block. Once performance had improved in one of the tasks it transferred to the other tasks. Improvement in performance to the ON-stimulus was found to extend over many more presentations than that to the OFF-stimulus.

Keywords: Apparent motion; Perceptual learning; ON-pathway; OFF-pathway

1. Introduction

Two types of ganglion cells in the mammalian retina specifically detect the polarity of changes in luminance. ON-centre cells increase their firing rate due to increase in luminance, but OFF-centre cells, in contrast, in response to decrease in luminance. The dendritic structures of these two types of cells in the retina, as well as their axonal target zones in the LGN are well separated (Wiesel & Hubel, 1966; Famiglietti & Kolb, 1976; Bolz, Rosner, & Wässle, 1982; Hubel & Livingstone, 1990; Kremers, Lee, Pokorny, & Smith, 1991). Motion of small, dark or bright objects generally results in both negative and positive types of luminance changes, because cells of both pathways are activated.

In an earlier study, we had developed an apparent motion stimulus selectively activating either the ON- or the OFF-pathway (Wehrhahn & Rapf, 1992). Two bright or dark vertical lines appear successively on a background of intermediate luminance. The lines stay on for about a second and are switched off simultaneously. Only onset asynchrony is created by this stimulus. For highly trained observers stimulated in the central fovea and for lines separated by around 3 arcmin, temporal thresholds measured with both these stimuli are between 3 and 5 ms for two bright lines and between 5 and 9 ms for two dark lines. Further increase of line distances of bright lines up to 10 arcmin leads to only small increments in thresholds, similar to experiments with bright lines on a dark background reported earlier (Westheimer & McKee, 1977). In contrast, for dark lines thresholds are significantly elevated already at a distance of 5 arcmin. At an angular distance of 3 arcmin, a sequence of a bright and a dark line, or vice versa, yields temporal thresholds well above 20 ms. Together with earlier results from other groups, these experiments indicate that the separation of ON- and OFF-pathways extends up to the level of local motion perception. Earlier evidence for motion mechanisms in humans preserving contrast polarity came from a study using dots of different contrast polarity in an apparent motion task (Shechter & Hochstein, 1990) and another report in which subjects were adapted to slow changes in one contrast polarity by means of a sawtooth conterphase grating. When exposed to a test pattern, which contained both contrast polarities, only the test compo-

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nent containing the unadapted change was visible (Mather, Moulden, & O'Halloran, 1991). This is consistent with results in global motion perception using random dot stimuli with dots of either equal or opposite contrast polarity (Edwards & Badcock, 1994; Croner & Albright, 1997; Snowden & Edmunds, 1999; van der Smagt & van de Grind, 1999).

Repeated presentation of visual stimuli may or may not lead to improved performance of subjects in that task (Ramachandran & Braddick, 1973; McKee & Westheimer, 1978; Fiorentini & Berardi, 1981; Bennett & Westheimer, 1991; Poggio, Fahle, & Edelman, 1992; Beard, Levi, & Reich, 1995, review by Wehrhahn, 2000). Different time scales were observed in which performance improved. For example slow perceptual learning in the perception of the direction of motion of a random dot pattern extending over more than 2000 presentations was reported earlier (Ball & Sekuler, 1982, 1987). Later experiments with moving random dots showed substantial improvement through practice within less than 300 presentations (Vaina, Sundareswaran, & Harris, 1995). Most other reports about perceptual learning in vision are roughly within the latter time frame.

Comparing perceptual learning of different tasks may yield information about the neural mechanisms underlying behavioral changes (Karni & Sagi, 1991; Ahissar & Hochstein, 1993). The experiments described here were designed to answer two questions: Do we find perceptual learning in apparent motion and, if so, do they apply equally to the two polarities of our apparent motion stimuli? We find that one-half of the observers tested substantially improve their performance in the course of at least 1960 presentations. The other observers were found to have relatively low thresholds at the outset of our study, and did not improve through the practice given in our experiments. Moreover, we report that improvement through practice of our two tasks proceeds in two qualitatively different time scales. Reports as a doctoral thesis (Rapf, 1996) and in abstract form (Rapf & Wehrhahn, 1993, 1994) about the results described in this paper had appeared earlier.

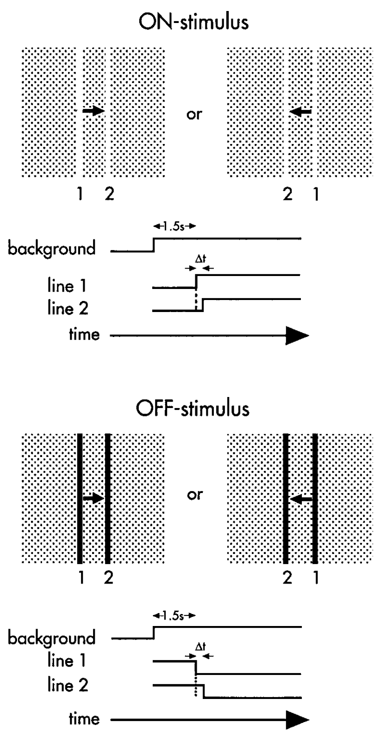

Fig. 1. Schematic depiction of the two stimuli used in the experiments and the temporal sequence in which they were presented. Angular distance between lines was 3 arcmin in all experiments. The onset asynchrony of the lines is varied.

2. Methods

The psychophysical methods used have been described previously (Wehrhahn & Rapf, 1992). Briefly, stimuli were generated on a monitor (HP 1345A) equipped with a fast phosphor. Signals on the monitor were controlled through an interface constructed by T. Kumar by a computer (IBM PC) generating a refresh rate of 500 Hz. Observers sat 3 m away from the monitor and viewed the stimulus presented to the fovea with both eyes using a head rest. Fixation was guided by four stationary LEDs outlining a square of 1.2° side length.

A bright (82 cd m^{-2}) rectangle 20 arcmin high and 22 arcmin wide appeared on the screen in the centre of the four LED's. After 1.5 s, the apparent motion stimulus was shown consisting of two vertical lines, each 20-arcmin long and 0.4-arcmin wide. The lines were separated by 3 arcmin in the horizontal plane and were both either brighter or darker than the rectangle (Fig. 1). Michelson contrast of lines was about 0.6 for both dark and bright lines. Onset asynchrony between the lines was varied; in each presentation and for all subjects tested, either the left or the right line led by 2, 8, 16, 22, 30, 36 or 44 ms at random. Timing was controlled by a quartz clock and calibrated by a high precision oscilloscope. The observer had to indicate the temporal order of the appearance of the lines by pressing either the left or the right button of a mouse. Observers were divided into two tantamount groups, one starting with 1960 presentations of ON-stimulus followed by 1960 presentations of OFF-stimulus and vice versa. In more detail, all observers viewed 40 blocks of 98 presentations each, with six to eight blocks on a single day and five to seven sessions distributed over 2–3 weeks. No error feedback was provided. Data for two successive blocks were accumulated and probit curve fitting of the resulting psychometric function yielded a threshold value and its 95% confidence interval for that asynchrony in which the observer correctly

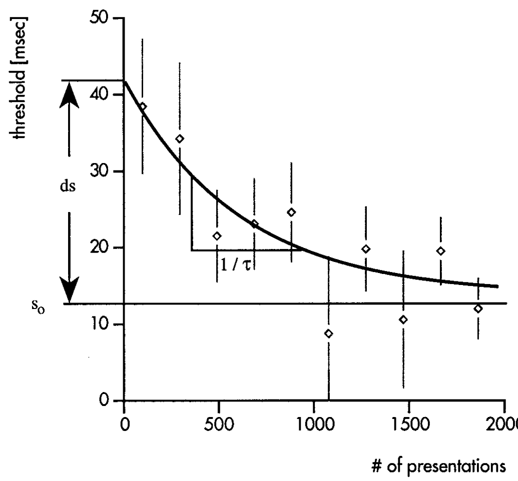

Fig. 2. Example for the threshold values determined from 196 subsequent presentations in one subject and the exponential function fitted to the data. Bars denote the 95% confidence interval. The three parameters (s_o, theoretical value reached when thresholds have stabilized; ds, difference between initial threshold and s_o; and τ, time constant) used are illustrated. Subjects whose ds was significantly different from 0 were categorized as having improved their performance through practice.

identified the direction of the presented sequence in 75% of the presentations.

Thresholds are plotted for each observer as a function of the number of presentations (Fig. 2 gives an example) and fitted with an exponential function: where S is the threshold (in ms) reached after 1960 presentations, ds the difference (in ms) between asymptotic (s_o) and initial threshold. N is the number of presentations required to improve threshold by a factor $1/e$. As the number of presentations increased observers could be classified into two categories. One group clearly improved during the 1960 presentations, the other one did not. Thresholds for corresponding trials were averaged across subjects for the two groups and both tasks. An analysis of variance was carried out for which observers had not been categorized yet with the factors 'number of blocks presented', 'task' and 'order of task' focussing on the interaction between task and order of task as outlined in the results section. An analysis of variance (ANOVA) was computed with a program using the algorithm designed by Keppel (1973).

All 26 subjects participating in the experiments had normal or corrected to normal vision and had never performed a psychophysical experiment.

3. Results

In Fig. 3A, average thresholds of those subjects are plotted whose performance over time improved with practice. The upper panel shows thresholds of seven subjects who had seen 1960 presentations of the ON-stimulus followed by the same number of presentations of the OFF-stimulus. Performance of this group improved by more than a factor of 2 during the first-half of the presentations. Note that the last threshold for the

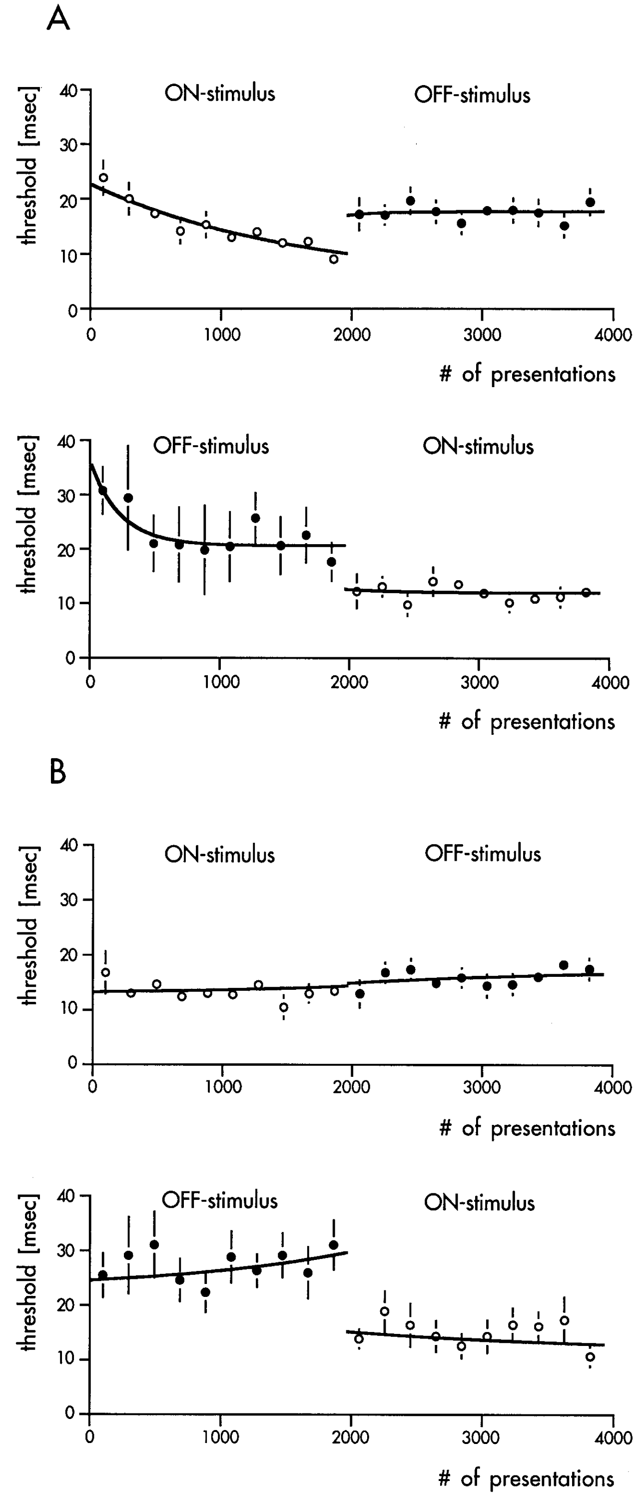

Fig. 3. Averaged psychophysical thresholds for the two tasks plotted; (A) for those observers showing improvement through practice (see Fig. 2) and (B) observers who did not show improvement with practice. Error bars indicate 95% confidence intervals.

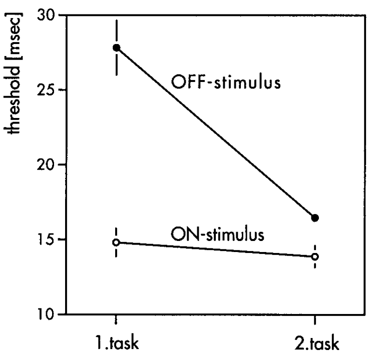

Fig. 4. Global averaged threshold values as a function of the task and the temporal sequence presented. Bars are 95% confidence intervals.

ON-stimulus determined (around 9 ms) obviously does not represent the asymptotic value. No further improvement was observed in the averaged thresholds of this group during the subsequent presentation of OFF-stimulus. In the lower panel of Fig. 3A, average thresholds of the four subjects are shown which saw the inverse stimulus sequence and whose performance improved with practice. For these observers thresholds stabilize at around 20 ms after less than 1000 presentations of OFF-stimulus. Subsequent presentation of the ON-stimulus yields threshold for these observers well comparable to those whose performance did not improve with practice (upper panel, Fig. 3B).

In the upper panel of Fig. 3B, average thresholds of the six subjects are shown who first saw the ON-stimulus followed by the OFF-stimulus and whose performance did not change over the whole period of the experiment. We think that the elevation of the first point can be attributed to the fact that subjects had to get accustomed to the general conditions of the psychophysical experiment like having their head in a chin rest etc. rather than to perceptual learning. For the nine subjects who first saw 1960 presentations of OFF-stimulus, even a slight increase in thresholds is found as can be seen in the lower panel of Fig. 3B. Due to the high variance in the data this elevation is not significant. Performance with ON-stimulus in this last group does not change for the number of presentations shown and — at around 16 ms — is slightly inferior to the performance of the four observers in the third plot whose performance to the first set of OFF-stimulus had improved with practice.

An ANOVA was carried out with factors task (ON-stimulus vs. OFF-stimulus), order of tasks (first ON- then OFF-stimulus vs. first OFF- then ON-stimulus), and number of blocks presented (block number 1, 2, 3, …). This yields a highly significant interaction between task and order of tasks $\{F(91, 24) = 10.047;\ P = 0.004\}$ (Fig. 4).There is no effect of the order of tasks for ON-motion with mean thresholds of 14.8 ± 0.9 and 13.9 ± 0.7 ms performed as first and second task, respectively. In contrast, mean thresholds for OFF-stimulus were higher by a factor of 1.7 when this task was performed first as compared with when it was performed for the second time. Subjects were not distinguished by category for this ANOVA.

4. Discussion

In an earlier paper, we had measured the performance of highly trained human observers in the task used in this study. The parameter varied was a range of angular distances between lines presented in succession. We found that the contrast polarity of two lines creating an apparent motion stimulus had effects on temporal thresholds. We concluded that ON- and OFF-pathways project to two separate neuronal substrates for the perception of local motion. In the experiments shown here, 26 observers were tested who had never done a psychophysical experiment and who were unaware of the goal of the study. Fig. 3 clearly shows that these naive observers can be subdivided into two different groups using the criterion outlined in Fig. 2. Irrespective of the sequence in which the two stimuli were presented observers of Fig. 3A improved their performance with practice while observers shown in Fig. 3B did not. Thresholds of the upper panel in Fig. 3B who first saw the ON-stimulus are conspicuously low already at the beginning of the experiment. This may be explained by assuming that these subjects have already had sufficient training to prevent any further improvement. This is likely because the subjects used their central fovea. Perceptual learning due to stimuli presented outside the fovea seemed much more common than inside (Beard et al., 1995; Ito, Westheimer, & Gilbert, 1998). Thresholds of the subjects who first saw OFF-stimulus were rather high indicating that it was very difficult for them to discriminate direction with stimulus. That is particularly conspicuous in view of the fact that highly trained observers display rather low thresholds for both these ON- and OFF-stimuli (Wehrhahn & Rapf, 1992).

An estimate of base line performance can be obtained by considering the respective first points (representing the first 196 presentations) in Fig. 3. It may be of interest to note here that we did not measure baseline performance before the experiments proper were started. As already mentioned, substantial improvements through practice within less than 300 presentations had been observed with moving random dots as well as in vernier acuity (Poggio et al., 1992; Vaina et al., 1995). Due to the rather local stimulus, our motion task bears some similarity to the vernier task.

The shapes of the learning curves in Fig. 3A differ qualitatively depending on the sequence of stimulus presentation. Thresholds for the OFF-stimulus reach stable values after less than 1000 presentations. Thresholds for ON-motion have not even reached their asymptote after 1960 presentations. Extrapolating the time course of the second curve yields stable values of around 5 ms after around 5000 presentations. This value corresponds to that found earlier in highly trained subjects (Wehrhahn & Rapf, 1992). This is consistent with earlier observations of improvement through practice in motion perception (Ball & Sekuler, 1982). Such a slow progress in performance is similar to that seen in binocular stereopsis (Coutant & Westheimer, 1993) and is qualitatively different from the time courses reported otherwise (review Wehrhahn, 2000). This could also mean that theoretical concepts like the HyperBF-algorithm used to describe fast perceptual learning of hyperacuity and color from a few examples (Hurlbert & Poggio, 1988; Poggio et al., 1992) must be modified to apply to the rather slow improvement observed here.

Surprisingly, after the two tasks have been switched between the two groups of observers (more precisely in the second data point of that block), all subjects independent of their task (ON vs. OFF) and their performance history (Fig. 3A vs. B) display low thresholds. Even if the detection thresholds are rather high at the end of the first task, thresholds observed in the second task appear to be almost invariably low. This means that the improvement once achieved by practicing one task is transferred to the other task. In a related experiment Liu and Weinshall (2000) found that subjects having practiced to see motion in one direction only, improved their performance in the other direction as well. The generalization process observed in our experiments must be located in a cortical area where the pathways carrying motion signals have converged with respect to contrast polarity, which is probably area MT (Croner & Albright, 1997). This generalization process also seems to be bound to the presentation of at least a few presentations of ON-stimulus.

We saw from the ANOVA results plotted in Fig. 4 that the sequence in which the tasks were presented was crucial for the performance in OFF-motion. It seems, therefore, that exposure to ON-motion after having practiced seeing OFF-motion plays a crucial role in the transfer from one task to the other. Earlier experiments had shown that the ON-pathway was dominant over the OFF-pathway with respect to the elaboration of local motion (Wehrhahn & Rapf, 1992). It is of ecological advantage to have two independent substrates to compute early motion. For example, it was shown some time ago that the motion sense of monkeys, whose ON-pathway had been blocked by a pharmocological agent, was not impaired. Contrast sensitivity in the perception of apparent motion seems to be higher towards bright as compared with dark stimuli.

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